

山毛榉科植物的起源和地理分布*

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THE ORIGIN AND DISTRIBUTION OF THE FAMILY FAGACEAE

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Abstract On the basis of unity of the phylogeny and the process of dispersal in plants, the origin and distribution of the fagaceous plants are discussed. For some important problems about the systematics of Fagaceae, the author proposes his point of views. The main conclusions are as follows:

The distribution pattern of genera: The living genera of Fagaceae are divided into four disjunct distribution patterns, i. e., 1. The genus of disjunct distribution between tropical Asia and tropical Central America; *Trigonobalanus*. 2. The genera of disjunct distribution between Asia and west of North America; *Lithocarpus*, *Castanopsis*. 3. The genera of disjunct distribution between Eurasia and North America; *Castanea*, *Fagus*. 4. The genus of disjunct distribution between Eurasia, North Africa and America; *Quercus*.

The distribution of species: Based on Takhtajan's opinion of phytochoria, about 880 living species of six genera in this family occur in 11 regions of three kingdoms. Among them, both genera and species are most abundant in the East Asian Region (5 genera, 261 species) and the Southeast Asian Region (4 genera, 283 species). Of living species, 541 are regionally endemic elements (excluding endemic species of *Quercus* in America, see Table 1), namely 61% of the total. In America and Europe, endemic species are mostly of neo-endemic nature because about 95% of them come from the advanced subgenus *Quercus*, however, those in Malaysia, Southeast Asian and East Asian Regions are of paleo-endemic nature. There are six genera, 320 species, about 40 subspecies and varieties in China. Southwest and south China are most abundant in species and Yunnan province is the richest in both genera and species (6 genera, about 176 species).

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Distribution patterns of the Fagaceae: As known at present, there are two distribution centres of the floristic region. Southern East Asia to northern Southeast Asia is determined as the main distribution centre, where occur not only the majority of genera and species, but also the primitive and advanced forms of genera and species; and southern Madrean to Caribbean region (Southwest U S A, Mexico, Central America) is the secondary distribution centre, where over half of the total species of the advanced genus *Quercus* are distributed, but of the other genera of Fagaceae, only one species is known occurring in Madrean and Caribbean Regions.

The place of origin: In tropical and subtropical regions, the evergreen fagaceous plants have several flushes a year. Northern Fagaceae are usually presumed to have a single flush, but in Nebraska of the United States, five deciduous species of *Quercus* were also observed to have as many as five flushes during a wet summer. It could be assumed as atavism if it is found in the deciduous oaks and should be used as evidence that the fagaceous plants originated from the tropical region. And both the primitive and advanced genera of Fagaceae, including the primitive infrageneric taxa (for example, *Lithocarpus elegans*, and the subgenus *Cyclobalanopsis* of *Quercus*) are mainly distributed in south and southwest China and north Indochina. Additionally, the living primitive genera of Hamamelidaceae which is usually considered phylogenetically closely related to Fagaceae are mainly distributed in above-mentioned region. So it is quite possible that in the region the tropical mountains with a dry season is the birth place not only for Hamamelidaceae but also for Fagaceae.

The time of origin: Nothofagaceae is recently treated as a sister group of Fagaceae. Its pollen, a kind of very distinct type (exine echinulate) occurred from the early Campanian of the upper Cretaceous, and the characteristic Castaneoid Tricolpoid Pollen are found from the Santonia and Santonia Campanian. So the original time of Fagaceae can be probably determined at the early period of the upper Cretaceous.

The routes of dispersal: The land bridges were very important to the distribution of fagaceous plants in upper Cretaceous and early Paleocene. When the climate and geographical conditions were very convenient, the fagaceous plants developed and distributed rapidly. From the original locality they entered America mainly by two routes: The plants of *Trigonobalanus*, *Lithocarpus* and *Castanopsis* were possibly distributed via Eurasia-Greenland-bridges (including many now-sunken islands in Atlantic Ocean) to America. The *Lithocarpus* fossils found from the Paleocene of Europe and Eocene of the North America confirms the presence of this dispersal route. But the deciduous oaks in the North America came from the East Asia via Bering-land-bridge. From North America, they extended to Central and South America.

The formation of the modern distribution pattern and reasons for this formation might be concluded as follows. The modern distribution pattern of living fagaceous plants is due to the results of continental drift, the glaciation effect, and biological characters of plants them-

具短尖头,常具腺体;木射线 1~2 细胞宽,木纤维具单纹孔(Shimaji, 1962);单珠被(Poole, 1952);叶缘具重锯齿和具腺体的毛被(Jones, 1986)。主张将南水青冈放在山毛榉科的学者则认为:壳斗才是山毛榉科区别于其它科的最根本的标准(Jenkins, 1993; Soepadmo, 1972)。笔者支持将南水青冈属提升为科的处理(Kuprianova, 1962),因此,本文采取狭义山毛榉科的概念分析其地理分布。

1 科的分布

全世界山毛榉科植物有 6 属,约 880 种,间断分布于欧亚大陆和美洲大陆(图 1),其分布格局与胡桃科(路安民, 1982)桦木科(陈之端, 1994)十分相似,均为北温带科,差别在于山毛榉科植物在热带亚洲有广泛的分布,有 4 属,约 160 种,(Soepadmo, 1972)。在欧洲,分布区的北界位于北纬 60°的卑尔根(Bergen)和圣彼得堡(St. Peterbury)(Axelrod, 1983)。在亚洲,分布区的北界位于北纬 56°的萨哈林岛(库页岛)。在北美洲,分布区的北界位于北纬 50°加拿大南部的温尼伯湖区(Axelrod, 1983),而分布区的南缘位于南纬 10°的新几内亚岛南端的莫尔兹比港。在南美洲,分布区仅限于赤道一侧的哥伦比亚的安迪斯山区。山毛榉科植物还从欧洲经地中海沿岸分布到了非洲北部的阿尔及尔和摩洛哥的最北端,非洲、南美洲的绝大部分地区以及大洋洲没有山毛榉科植物的记载。

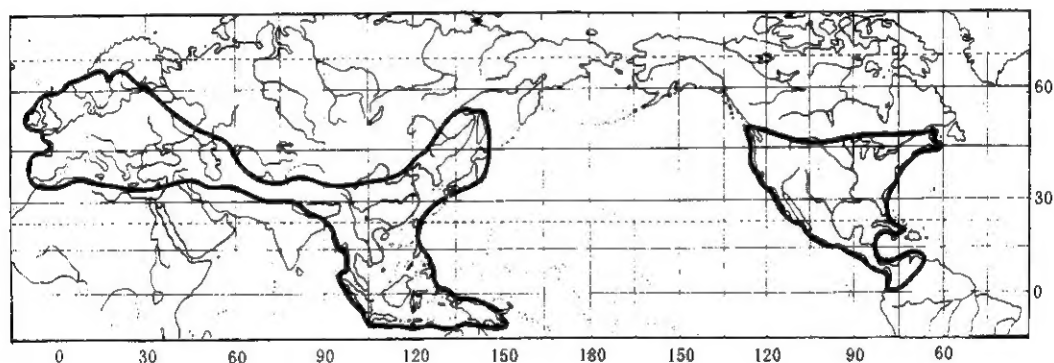


图 1 山毛榉科植物的地理分布

Fig. 1 Distribution of the Fagaceae (redrawn from soepadmo, 1972, excl. voth of agus)

2 属的系统位置及分布式样

2.1 柯属 *Lithocarpus* Bl. 是现存山毛榉科植物中最原始的属。分布区从尼泊尔、不丹、孟加拉国、印度东北部向东北经中国西藏东南部,黄河以南最北端到韩国南部及日本南部的九州岛(北纬 32°),向东南经缅甸、泰国、中南半岛、大巽他群岛、菲律宾群岛到新几内亚岛,大约位于北纬 35°,南纬 10°,东经 85°~150°;仅一种(*L. densiflorus*)分布在美国西南部的加利福尼亚州和俄勒冈州西南部,而形成了现在的亚洲东南部与北美洲西南部的间断分布格局(图 2)。柯属共 279 种,马来西亚、大巽他群岛、菲律宾群岛共 104 种(Soepadmo, 1972),其中马来西亚、加里曼丹岛几乎集中了该区域内 75% 的种类(共 77 种)。中国有 122 种,1 亚种,14 个变种(含台湾 14 种),其中绝大多数种分布在中国南部和

(Crepet *et al.*, 1989)。古孢粉证据表明,它们到达南美的时间大约在更新世(Van Der Hammen *et al.*, 1973)。在山毛榉科植物分化和散布时,至少在新生代古新世之前,马来西亚区的诸岛屿还未形成,由于该区位于欧亚大陆的最南端,气候偏热,所以喜温性的栗属、水青冈属及栎属中的栎亚属植物向该地区的散布受到了限制,这可能是该区没有上述植物类群分布的主要原因,而喜热的柯属、锥属、三棱栎属及栎属中的青冈亚属则在本区得以生存和发展起来。

唯一与上述两条迁移路线相悖的是柯属植物的大化石较早出现在北美洲的事实。这可能有两种解释。第一,北美与世界上其它地区(欧洲除外)相比具有保存这些化石材料的良好条件(包括地质的和气候的条件);第二,则是我们对亚洲的东南部,尤其是中国南部、西南部和中南半岛北部这一关键地区第三纪古植物化石群的研究不够深入。此外,也不排除北美化石材料在鉴定上的问题。

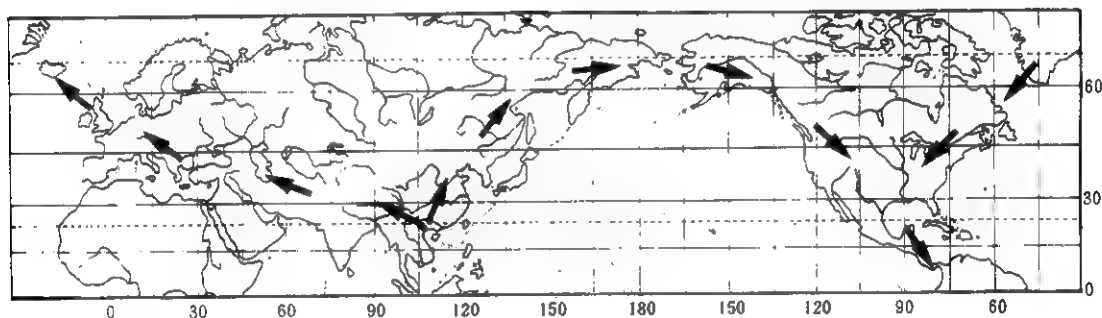


图 8 山毛榉植物从起源地到美洲两条可能的迁移路线(实心点表示起源地)
Fig. 8 Two Possible dispersal lines of the fagaceous plants from their birth locality to America
(The birth locality shown in solid dot)

4.5 现代分布式样形成的原因

植物现代分布的格局是环境因素(包括地质、气候因素)作用于植物以及植物自身对于环境影响作出反应的综合表现。山毛榉科植物的现代分布区包括 4 种大的洲际间断分布类型(见属的分布一节)以及许多小的岛屿状间断分布(如我国台湾和海南岛、日本及我国大陆之间的间断分布),而上述间断分布形成的原因可以归结为三个方面的因素。首先是大陆漂移形成的海陆相应位置的变化,这样就造成了大陆与大陆之间,大陆与沿海的岛屿间,以及岛屿与岛屿间的间断分布,这是形成山毛榉科植物 4 种大的洲际间断分布的主要原因。其次是气候条件的改变,第三纪末期上新世柯属植物在欧洲大陆上的逐渐消亡(Kvacek *et al.* 1989),极有可能是受到当时气候变寒冷的影响。美国加利福尼亚州和俄勒冈州的特殊生境使得喜温热的柯属和锥属各有一种植物能残存下来。冰川对欧亚大陆的影响使得中国秦岭以北到整个欧洲的广大地区中的三棱栎属、柯属以及锥属植物全部绝灭。除此之外,植物自身的生物学特性以及对于不良环境的适应能力也是决定植物的分布区形成的重要原因。山毛榉科植物中的原始类群柯属以及锥属中的大部分种类果实为第二年成熟。雌花当年春天发出,但其大孢子母细胞的形成则在翌年春天,即胚珠的发育推迟了整整一年。生活史周期的延长对于植物的繁衍与发展显然是一种制约因素,这是上

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